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COMPARATIVE STUDIES ON THE POLLINATION BIOLOGY OF *DARWINIOTHAMNUS TENUIFOLIUS* (ASTERACEAE) AND *PLUMBAGO SCANDENS* (PLUMBAGINACEAE) ON PINTA ISLAND AND SANTA CRUZ ISLAND, GALAPAGOS

Conley K. McMullen

Department of Biology and Chemistry, West Liberty State College, West Liberty, West Virginia 26074 U.S.A.

&

Diane M. Viderman

190 Scenery Hill, Wellsburg, West Virginia 26070 U.S.A.

ABSTRACT

Fruit set and flower visitors of *Darwiniothamnus tenuifolius* (Asteraceae) and *Plumbago scandens* (Plumbaginaceae) were compared on Pinta Island and Santa Cruz Island, Galapagos, Ecuador. Results suggest that autogamy was favored during the initial colonization by these species. This mode of reproduction may now be supplemented by nonautomatic selfing and cross-pollination due to the presence of various flower visitors.

KEY WORDS: Pollination, Galapagos Islands, Ecuador, Asteraceae, *Darwiniothamnus tenuifolius*, Plumbaginaceae, *Plumbago scandens*

INTRODUCTION

In 1964, an unprecedented event in the history of Galapagos Islands research took place. This was the Galapagos International Scientific Project. For several weeks, the combined talents of botanists, zoologists, geologists, and many others were brought together in an attempt to more intimately know

the natural history of these Islands. Robert L. Usinger was among the entomologists who attended. Afterwards, he wrote of the "challenge to discover how the various animals and plants have worked out their destinies together" (Usinger 1972:249). Toward this end, E. Gorton Linsley (1966) compiled the first list of pollinating insects in the Galapagos Islands. This was followed by a detailed study of the pollination behavior of the endemic carpenter bee, *Xylocopa darwini* Cockerell (Hymenoptera: Apidae) (Linsley *et al.* 1966).

Other studies on the pollination of Galapagos angiosperms have followed (Rick 1966; Grant & Grant 1981; Aide 1986; McMullen 1985, 1986, 1987, 1989, 1990; Elisens 1989; McMullen & Close 1993). Most recently, a list of flower-visiting insects of the Galapagos Islands was compiled by McMullen (1993). This list was obtained from records in the scientific literature, as well as from personal observations conducted in the field during the summer of 1990. However, the relative importance of each visitor was not discussed. As the author suggested, details should be sought among the literature cited, or in future publications. The present paper will provide these details for two of the angiosperms mentioned in McMullen (1993).

METHODS

The two species treated here are *Darwiniothamnus tenuifolius* (Hook. *f.*) Harling (Asteraceae), an endemic shrub; and *Plumbago scandens* L. (Plumbaginaceae), a nonendemic native herb. The corymbiform inflorescences of *D. tenuifolius* are composed of heads with both disc and ray flowers. The yellow disc flowers are perfect and fertile, while the white ray flowers are pistillate and fertile. These inflorescences possess a mildly sweet odor. The white perfect flowers of *P. scandens* are arranged in paniculate spikes. They have little apparent scent.

Field work for the first part of this research was conducted on the southeastern slope of Pinta Island from 23 Jun - 26 Jul 1990. The study site for *Darwiniothamnus tenuifolius* was located at ca. 518 m altitude. Two sites were chosen for *Plumbago scandens.* One was located at 213 m, the other at 533 m.

Bagging experiments were conducted to determine if the species are autogamous (automatic self-pollinators). Fruit yields were compared for inflorescences completely isolated from insects (bagged), and others that were exposed to potential pollinators before being covered (open-pollinated).

Observations were made to determine what insects are visitors to the flowers of each species and might act as pollinators. *Darwiniothamnus tenuifolius* observations lasted 36 hours over four days. Those of *Plumbago scandens* lasted 40 hours during five days. Information such as how many visits were made and how long each visit lasted was obtained. The maximum time allowed for observing an insect during any one visit was 15 minutes. After this, the insect

was either captured, or another observation was begun so as not to spend an excessive amount of time watching one individual.

Similar studies were undertaken on the southern slope of Santa Cruz Island from 31 Jul - 10 Aug 1990. The study site for *Darwiniothamnus tenuifolius* was located at 632 m altitude near the craters known as "Los Gemelos." *Plumbago scandens* sites were located at 5 m altitude near Hotel Galapagos, and at 91 m altitude ca. 4 km north of Puerto Ayora on the road to Bella Vista. No bagging experiments were conducted as this information was available from previous studies performed in 1983-84 (McMullen 1987). All other observations and measurements were performed. However, the time spent observing visitors on this island was less than on Pinta (six hours during one day for both *D. tenuifolius* and *P. scandens*). Once again, this was due to the fact that research had previously been performed on Santa Cruz.

Voucher specimens of the plants were collected and deposited in the Charles Darwin Research Station herbarium (CDS). Specimens of each insect visitor were also collected and the majority of these are now part of the station's reference collection. Some duplicate specimens are housed at the Systematic Entomology Laboratory, United States Department of Agriculture in Beltsville, Maryland, and at Carleton University, Ottawa, Ontario.

RESULTS

Bagged inflorescences produced fruits for *Darwiniothamnus tenuifolius* and *Plumbago scandens* on Pinta and Santa Cruz (Table 1). Open-pollinated flowers of *P. scandens* produced a higher percentage fruit set than bagged flowers on both islands. The opposite was true for *D. tenuifolius* on Pinta.

Several flower visitors were recorded during this study and the insects visiting a particular plant on Pinta were often quite different from those visiting the same species on Santa Cruz (Table 2). *Darwiniothamnus tenuifolius* was visited most frequently on Pinta by a species of *Goniozus* (Hymenoptera: Bethylidae) (127 visits, 22,722 seconds). Pollen was seen on the abdomen of one such individual. A species of *Olcella* (Diptera: Chloropidae) made slightly fewer visits (112), but for a total of 28,422 seconds. *Atteva hysginiella* Wallengren (Lepidoptera: Yponomeutidae), an *Orthoperus* species (Coleoptera: Corylophidae), and *Lepidanthrax tinctus* Thomas (Diptera: Bombyliidae) also made visits to this plant. Of the twelve *A. hysginiella* individuals, one was seen with pollen on its antennae. *Goniozus* and *Olcella* individuals were the only visitors to stay on an inflorescence for longer than 15 minutes.

On Santa Cruz, *Darwiniothamnus tenuifolius* was visited most often by an unidentified moth (Lepidoptera: Tortricidae) (22 visits, 4,090 seconds). It was also visited by *Toxomerus crockeri* Curran (Diptera: Syrphidae), *Darwinysius marginalis* Dallas (Hemiptera: Lygaeidae), *Urbanus dorantes galapagensis* Williams (Lepidoptera: Hesperiidae), *Xylocopa darwini*, and another

Table 1. Bagging experiment results. Those for Santa Cruz are based on studies performed in 1983-84 (McMullen 1987).

	Darwiniothamnus tenuifolius		
	# Heads Tested	# Fruits Set	# Fruits per Head
Bagged			
Pinta	998	32,810	32.88
Santa Cruz	36	250	-
Open-Pollinated			
Pinta	990	24,799	25.05
Santa Cruz	47	250	-

	Plumbago scandens		
	# Flowers Tested	# Fruits Set	% Fruits Set
Bagged			
Pinta	554	70	12.64
Santa Cruz	57	30	52.63
Open-Pollinated			
Pinta	742	313	42.18
Santa Cruz	95	58	61.05

Table 2. Insect visitors. Visitation times are in seconds. Total refers to the time of all visits combined. N refers to the number of visits.

	Total	Mean	SD	N
Darwiniothamnus tenuifolius[1,2]				
Pinta				
Olcella sp.[3] (Diptera)	28,422	253.77	277.12	112
Goniozus sp.[3] (Hymenoptera)	22,722	178.91	198.36	127
Atteva hysginiella[1] (Lepidoptera)	1,664	138.67	134.33	12
Orthoperus sp.[3] (Coleoptera)	188	94.00	19.80	2
Lepidanthrax tinctus[3] (Diptera)	160	20.00	27.37	8
Santa Cruz				
Moth[3] (Lepidoptera: Tortricidae)	4,090	185.91	177.64	22
Toxomerus crockeri[1] (Diptera)	1,062	88.50	86.88	12
Darwinysius marginalis[3] (Hemiptera)	791	87.89	85.91	9
Moth[3] (Lepidoptera: Gelechioidea)	90	-	-	1
Urbanus dorantes galapagensis[3] (Lepidoptera)	23	3.29	2.14	7
Xylocopa darwini[1] (Hymenoptera)	2	-	-	1
Plumbago scandens[2,5]				
Pinta				
Leptotes parrhasioides[6] (Lepidoptera)	543	9.53	13.13	57
Cardiocondyla nuda[3] (Hymenoptera)	491	81.83	51.58	6
Lepidanthrax tinctus[3] (Diptera)	10	2.50	1.91	4
Naucles sp.[3] (Coleoptera)	Not Timed, Night Visitor			
Ornebius erraticus[3] (Orthoptera)	Not Timed, Night Visitor			
Paratrechina sp.[1] (Hymenoptera)	Not Timed, Night Visitor			
Santa Cruz				
Phoebis sennae (Lepidoptera)	641	3.08	2.31	208
Leptotes parrhasioides (Lepidoptera)	143	15.89	25.06	9
Urbanus dorantes galapagensis[3] (Lepidoptera)	13	-	-	1
Xylocopa darwini[4] (Hymenoptera)	1	-	-	1
Wasmannia auropunctata[4] (Hymenoptera)	Not Timed			

[1] Flowers recorded for the first time as visited by insects in the Galapagos Islands.

[2] Flowers recorded for the first time as visited by *X. darwini*.

[3] Insect recorded for the first time as a flower visitor in the Galapagos Islands.

[4] Insect recorded for the first time as a flower visitor to this plant species.

[5] Flowers recorded for the first time as visited by insects on Pinta Island.

[6] Insect recorded for the first time as a flower visitor on Pinta Island.

moth (Lepidoptera: Gelechioidea). There were actually many more Tortricidae moths, *T. crockeri*, and *D. marginalis* present than could be accurately timed, so only a fraction of the activity that took place is recorded.

Leptotes parrhasioides Wallengren (Lepidoptera: Lycaenidae) was the most common visitor to flowers of *Plumbago scandens* on Pinta (57 visits, 543 seconds). Other visitors included *Cardiocondyla nuda* Mayr (Hymenoptera: Formicidae), *Lepidanthrax tinctus*, a species of *Naucles* (Coleoptera: Scraptiidae), *Ornebius erraticus* Schudder (Orthoptera: Gryllidae), and a species of *Paratrechina* (Hymenoptera: Formicidae). The latter three were night visitors, and were not timed.

On Santa Cruz, *Plumbago scandens* was visited most frequently by *Phoebis sennae* (Lepidoptera: Pieridae) (208 visits, 641 seconds). Also making visits were *Leptotes parrhasioides*, *Urbanus dorantes galapagensis*, *Xylocopa darwini*, and *Wasmannia auropunctata* (Hymenoptera: Formicidae). Flowers of this species were previously recorded as being visited on Santa Cruz by *L. parrhasioides* and *P. sennae* (McMullen 1986, 1990).

DISCUSSION

Darwiniothamnus tenuifolius is at least facultatively autogamous on both Pinta and Santa Cruz. With the level of insect activity observed at these plants, the open-pollinated inflorescences might be expected to produce more fruits than the bagged inflorescences. This was not the case, probably because the open-pollinated flowers were exposed to predation before being isolated with pollination bags. Finches were observed on several occasions feeding on the flowers and fruits of this species. In addition, due to differing rates of maturation within a corymbiform inflorescence, the fruits of some heads fell before the flowers of others had reached anthesis. Thus, some fruits were lost before the entire inflorescence could be bagged.

From the timed observations, a species of *Olcella* and a species of *Goniozus* appear to be most important as pollinators of *Darwiniothamnus tenuifolius* on Pinta Island. However, it should be noted that *Atteva hysginiella* seemed to be much more common during casual observations than during the timed periods. Perhaps this insect was more aware of the observers, and avoided the plants at these times. Of the two visitors, *Olcella* and *Goniozus*, the latter may be more important in promoting cross-pollination since it spends less time on any one inflorescence. Three insect species may be important pollinators of *D. tenuifolius* on Santa Cruz. These are a Tortricidae moth, *Tozomerus crockeri*, and *Darwinysius marginalis*. Based on the above logic, the latter two may be more useful as cross-pollinators.

Plumbago scandens also produced fruits autogamously on both islands. Open-pollinated inflorescences showed a greater fruit set than bagged inflorescences. This would be expected given the insect activity during the timed

observations, and suggests that the insect visitors may be important pollen vectors. However, crosses on Santa Cruz did not produce any fruits (McMullen 1987). Perhaps these insects are more important in effecting maximum selfing, while outcrossing is negligible.

Darwiniothamnus tenuifolius was newly reported as having its flowers visited by insects in the Galapagos Islands. *Plumbago scandens* was recorded for the first time as having its flowers visited by insects on Pinta Island. In addition, *D. tenuifolius* and *P. scandens*, were newly reported as having their blossoms visited by *Xylocopa darwini*.

Eleven of the insects in Table 2 were recorded for the first time as visiting flowers in the Galapagos Islands, while one was newly recorded as visiting flowers on Pinta Island. Two insects were newly reported as flower visitors to *Darwiniothamnus tenuifolius*, and three were newly reported as flower visitors to *Plumbago scandens*. Although pollen was not observed on all of the visitors, the high level of activity within flowers for many of them suggests that they may be functioning as pollinators to some extent. The fact that many of the visitors were lepidopterans is significant since these insects are common pollinators on the mainland. This adds support to their possible role as pollen vectors in the Galapagos Islands.

In summary, the results of this study support the hypothesis that autogamous angiosperms were favored in the initial colonization of the Galapagos Islands (Rick 1966; McMullen 1987). This mode of reproduction may now be supplemented by nonautomatic selfing and cross-pollination due to the presence of various flower visitors. One of the more revealing discoveries of this research is the fact that, although few when compared to mainland standards, more insects visit flowers in this archipelago than previously believed.

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